ON THE PUERULUS STAGE OF SOME SPINY LOBSTERS (PALINURIDAE)

By ISABELLA GORDON

SYNOPSIS

The paper includes a key to the determination of the adult Palinurid genera to which the known post-larvae are referable, descriptions and figures of the Puerulus stage of several species of the genus *Panulirus* and notes on the Puerulus of the European Spiny Lobster. In an appendix the range of variation in the adults of the species *Panulirus homarus* (L.) is discussed.

INTRODUCTION

In March, 1952, I received from Hugh Copley, Esq., Fish Warden, Nairobi, an almost complete and beautifully preserved specimen of the Puerulus stage of a Palinurid. The antennae were intact, and the most striking feature of the post-larva was the dark brown spatulate apex of the long flagellum. A very similar Puerulus has recently been described in a Japanese journal which is not yet available in this country ; as the text is mostly in Japanese a description in English seems essential. A number of Pueruli from the Marquesas and Coiba were found in undetermined collections in the British Museum and they are also described in the following short paper. All these post-larvae proved to belong to the genus *Panulirus*, and it has been possible to refer most of them to their respective adult species. All possess a pair of long, backwardly directed spines at the posterolateral angles of the thoracic sternum (near the bases of the last pair of walking legs). All agree, moreover, in having the exopodite of maxilliped 3 vestigial, and therefore belong to species in which that exopodite is lacking in the adult. The material from the Marquesas is referable to either *Panulirus homarus* (L.) or the closely related *P. dasypus* (Latr.) and, in an appendix, I discuss my reasons for believing that these two may belong to one variable species.

In the Puerulus referred to *P. argus* (Latr.) by Gurney (1942, p. 234, fig. 93) the posterolateral thoracic spines are replaced by blunt nodules, and the exopodite of maxilliped 3 is rather longer than the ischium of the endopodite. The posterolateral spines are absent in *Puerulus pellucidus* (Ortmann), which has been referred to *Panulirus japonicus* (von Siebold)—see synonymy in Holthuis, 1946, p. 111, and Nakazawa, 1917.

At the present time the post-larva is known for only four genera of the Palinuridae, namely, *Palinurus* Fabr., *Panulirus* White, *Jasus* Parker and *Justitia* Holthuis. I have examined Pueruli belonging to each of the first three genera but that of *Justitia* is known only from a single specimen collected by the " Blake." It was first described as the " *Puerulus* d'Agassiz," referable to *Palinurus longimanus* H. M.-Edw. by Bouvier (1913, pp. 82 and 87 ; 1914, p. 187 ; and 1925,

p. 442, pl. 8, fig. 1), and Bouvier's figure has been reproduced by Schmitt (1935, p. 173, fig. 37). Holthuis erected the genus *Justitia* for *J. longimana* (H. M.-Edw.) and its variety *mauritiana* (Miers) in 1946, p. 115.

In the British Museum collection are the three specimens—Phyllosoma, Phyllosoma with the Puerulus in the act of disengaging itself, and Puerulus—of *Palinurus vulgaris* Latr. figured by Bouvier (1914, figs. 1, 2, and 3–6). Bouvier's sketch of the carapace of the Puerulus is not very accurate as to the anterior spines, the supraorbital spines especially being much more prominent than in the actual specimen (reg. no. 1914.12.17.4). I take this opportunity of refiguring the anterior part of the carapace and the antennule (Fig. 1*a*, *b* and *c*) for comparison with those of *Jasus* (Fig. 1*d* and *e*) and of *Justitia* as figured in Bouvier, 1925, pl. 8, fig. 1 (which appears to be accurate). Incidentally, Holthuis says that the common European "langouste" should be known as *Palinurus elephas* (Fabr.), which antedates *vulgaris* Latr.

I also give a key to the determination of the adult genera to which the post-larvae are referable ; it is more detailed than that given by Bouvier (1913, p. 87), but for the characters of the Puerulus of *Justitia* I have had to rely on Bouvier's figure and descriptions. I am not sure whether the antennae are intact, but if so they do not exceed 1·5 times the body length.

Key to the Determination of the Adult Genera to which the Post-larvae are Referable

1. Antennular flagella distinctly shorter than the peduncle, outer much more robust than the inner (Fig. 1*a* and *d*). Anterior margin of the antennular[1] tergum much narrower than the space between the tips of the supraorbital spines. Rostrum well formed or rudimentary (Fig. 1*a* and *d*). The "brevicornis" group.

    A. Exopodite of maxilliped 3 long, with multi-segmented flagellum. Posterolateral spines present on several of the somites of thoracic sternum. Rostrum rudimentary.

        1. Supraorbital spines denticulate on upper margin ; plate formed by these spines and the rostrum broad and advanced so as to conceal the eye-stalks, the corneae visible laterally. Three pairs of spinules on thoracic sternum. Distinct median carina on carapace and abdominal somites 2–5. Only a few spines on carapace near the orbits. Second segment of antennular peduncle equal to third
        Justitia Holthuis.

[1] The antennal tergum of some authors.

Fig. 1. *Palinurus elephas* (Fabr.) = *vulgaris* Latr. The Puerulus figured by Bouvier, 1914, p. 288, fig. 6. (*c.l.* = 7·5 mm.). *a*. Anterior part of carapace, in dorsal aspect, with left antennule and antennal peduncle. *b*. Right anterolateral spine with the two spines immediately behind it, more magnified. *c*. Left antennule more magnified. *Jasus lalandei* (H. M.-Edw.). Puerulus from "Discovery" Stn. 101, 15/x/26 (*c.l.* = 9·5 mm.). *d*. Anterior part of carapace in dorsal aspect, with left antennule and antennal peduncle. *e*. Left antennule more magnified.

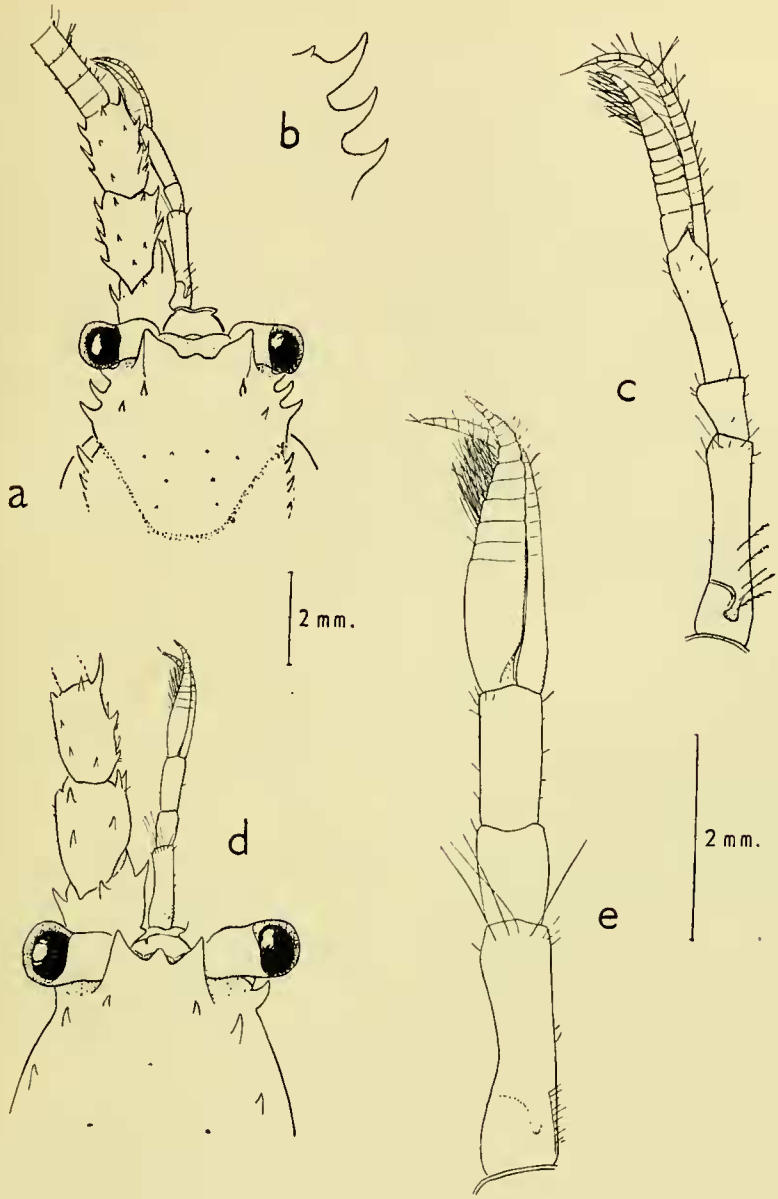

FIG. 1.

2. Supraorbital spines not denticulate on upper margin ; plate formed by these spines and the rostrum narrower and less advanced, most of eye-stalks visible (Fig. 1*a*). Four pairs of spinules on thoracic sternum. No median carina on carapace or abdomen. Carapace spiny, three spines at each anterolateral angle and a longitudinal row of spinules replacing each lateral carina. Second segment of antennular peduncle shorter than third (Fig. 1*c*). [Antenna not quite 1·5 times the body length and tapering distally. First pair of pereiopods more robust than the others.] . . *Palinurus* Fabr.

B. Exopodite of maxilliped 3 short, without flagellum. No posterolateral spines on thoracic sternum. Rostrum well developed (Fig. 1*d*). [Supraorbital spines not denticulate on upper margin ; plate formed by these and the rostrum narrow, moderately advanced, but most of eye-stalks visible. One spine at anterolateral angle of carapace. No median, but two lateral carinae on posterior two-thirds of carapace. Second segment of antennular peduncle rather shorter than third (Fig. 1*e*). Antenna not quite 1·5 times the body length and tapering distally. First pair of pereiopods more robust than the others.] . . . . . *Jasus* Parker.

II. Antennular flagella at least as long as the peduncle, outer not much more robust than the inner (Figs. 2*a*, 5*a*, *c*). Anterior margin of antennular[1] tergum as wide as the space between the tips of the supraorbital spines. Rostrum absent. The " longicornis " group. [Usually a large pair of posterolateral spines on last somite of thoracic sternum and three carinae on the carapace. One (occasionally two) spine(s) at anterolateral angle of carapace. Second segment of antennular peduncle equal to third. First pair of pereiopods not more robust than the others (Fig. 7*b*, *c*).] . *Panulirus* White.

a. THE PUERULUS STAGE OR POST-LARVA OF PANULIRUS sp.

(Figs. 2*a* ; 3 ; 7*c*)

Material. Taken in trawl by M.F.V. " Menika " on Leopold Reef ground, Malindi, Kenya Colony, in 10 to 20 fms.—one specimen, presented by H. Copley, Esq., Fish Warden, Nairobi. March, 1952.

Measurements : Length of body 21·5 mm. ; Length of carapace 8 mm. ; Length of antenna (complete) 45 mm.

Description. The specimen had been preserved in formalin and the body, though transparent in life, was apparently tinged with reddish brown. When received it was complete except that pereiopods II and V on the right side were missing. The most striking feature of the post-larva is the enormously long antennae, measuring just over twice the body length. The flagellum ends in a flattened oar-like expansion which is all the more conspicuous because the last 7 or 8 segments of the spatula are brown in colour (Fig. 3*a* ; brown portion stippled). A narrow

[1] See footnote on p. 18.

Fig. 2. *a*. Puerulus of *Panulirus* sp. from Kenya, in dorsal aspect, most of the antennal flagella omitted. *b*. Distal portion of antenna of the last stage Phyllosoma of *P. homarus* (L.) from the Marquesas. *c* and *c'*. Distal segments of incomplete antennal flagella of two Pueruli of *P. homarus* (L.) from the Marquesas. *d*. Terminal segments of antennal flagellum of the Puerulus of *P. argus* (Latr.) from Bermuda.

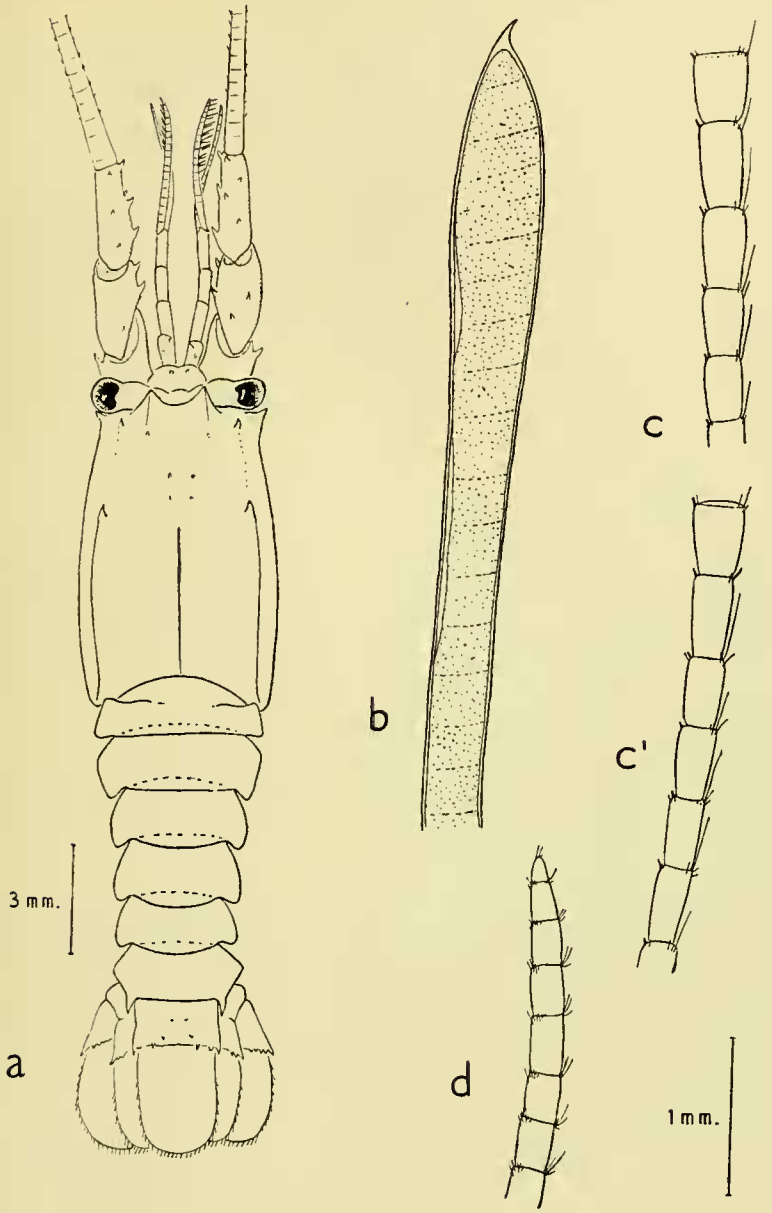

FIG. 2.

band of the brown colour, a trifle paler, is present about one-third of the way along the flagellum (i.e., at distal end of proximal third).

Fig. 2*a* represents the post-larva in dorsal aspect, with the greater part of the antennal flagella omitted. The *carapace* measures 8 mm. from the tip of the supraorbital spine to the posterior margin ; it bears only two pairs of spinules in addition to that at each anterolateral angle. The anterior pair is situated immediately behind the eyes ; the posterior pair is some distance behind, one spinule at the anterior end of each lateral carina. If the specimen is examined carefully under a binocular microscope, three pairs of incipient spinules can be detected situated between the anterior and posterior pairs of spinules, i.e., two median (gastric) pairs a short distance in front of the median carina, and another pair posterior to the carinae on the supraorbital spines. The three longitudinal carinae on the posterior two-thirds of the carapace are not very clearly seen in dorsal aspect, but in profile they stand out clearly : Each lateral carina seems to be continued forwards to the anterior pair of spinules ; the incipient spinules appear as thickenings of the chitin, so that the median carina seems to bifurcate and to be continued forwards to the base of each rostral horn. A pair of incipient spinules is present on the antennular tergum, near the anterior margin. A thin carina, not visible in dorsal aspect, runs parallel to the lateral edge of the carapace. The cervical furrow is not very apparent at this stage.

The *thoracic sternum* is very similar to that of the Puerulus of *Panulirus regius* B. Capello figured by Bouvier (1917, pl. ix, fig. 9) ; in addition to the pair of large, backwardly-directed spines on the last somite, near the bases of pereiopods V, there are blunt lobules, which diminish in size anteriorly, at the postero-lateral angles of each of the three preceding somites. Bouvier's fig. 9 does not show these, but that on the penultimate somite is visible in lateral aspect in his fig. 10. The thoracic ganglia are clearly visible through the thin integument.

The *abdomen* and tail fan present no unusual features. No groove is present on any of the terga parallel to the posterior margin, but the anterior margin of the succeeding somite is visible through the thin chitin and is represented by a broken line in Fig. 2*a*. The pleura of somites 2 to 6 each possesses a sharp, backwardly directed spine which is not visible in dorsal aspect.

The *antennule* is short, extending only a little way beyond the antennal peduncle (Fig. 2*a*) ; the external flagellum is the more robust, a trifle longer than the internal and beset with special sensory setae on all but the proximal 6 or 7 segments. Each flagellum has 18 or 19 segments. The details of the peduncle are shown in ventro-lateral aspect in Fig. 3*b* and *c*, of the basal segment in dorsal aspect in Fig. 3*d*. All the setae are very finely plumose, as are those forming what Gilchrist (1920, p. 198, fig. 13) calls the " antennular screen." In the Puerulus of *Jasus lalandei* (H. M. Edw.) Gilchrist shows these setae as heavily plumose. The basal segment

FIG. 3. Puerulus of *Panulirus* sp. from Kenya. *a*. Terminal portion of antennal flagellum, to show the spatulate apex. *b*. Antennal and antennular peduncles, in ventro-lateral aspect. *c*. The latter further enlarged. *d*. Basal segment of antennular peduncle, in dorsal aspect. *e*. Pleopod on second abdominal somite, with most of the long setae omitted, and apex of *appendix interna* further enlarged.

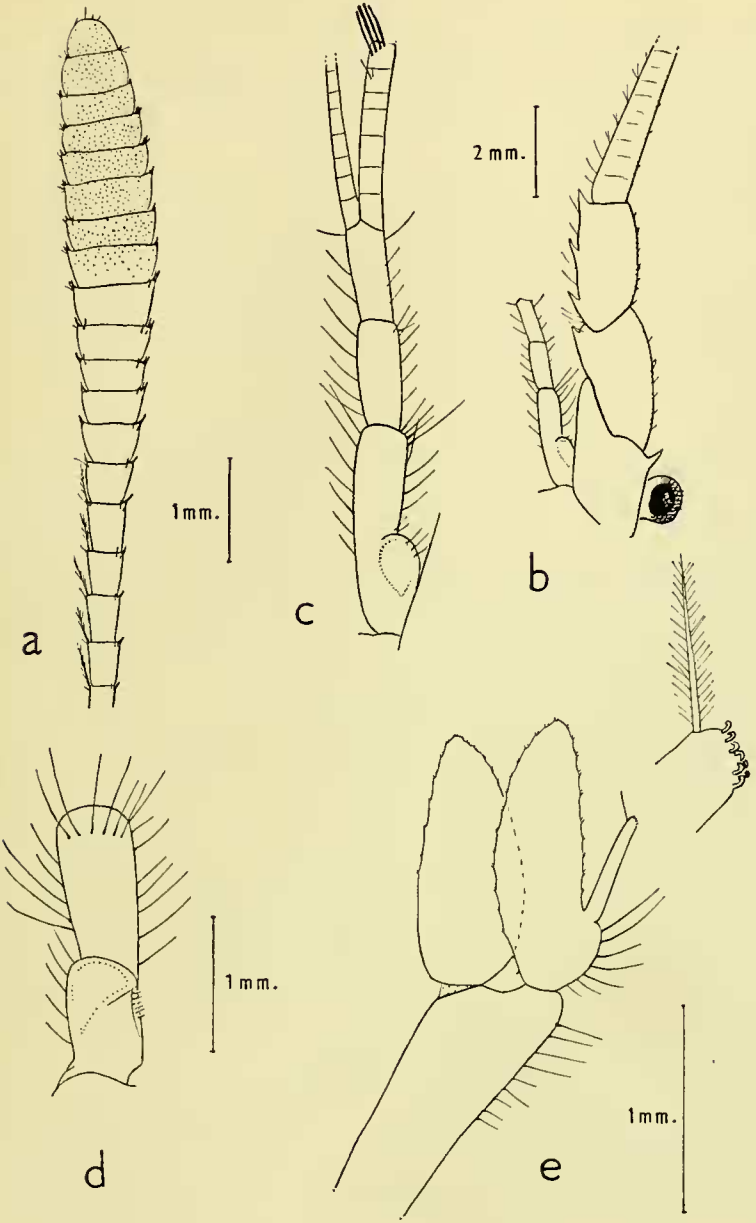

FIG. 3.

of the peduncle is equal in length to the sum of the other two segments ; the statocyst is conspicuous but without any statolith.

The details of the *antennal peduncle* are shown in Fig. 2*a* in dorsal and in Fig. 3*b* in ventrolateral aspects. The spatulate apex of the long flagellum is represented in Fig. 3*a*, the shaded terminal segments being, in the preserved specimen, brown in colour.

The *eyes* are large and conspicuous, extending as far as the anterolateral spinose angles of the carapace.

The *external maxillipeds* are widely separated basally ; when extended they reach the anterior margin of the antennular somite ; a minute trace of an exopodite is present. The mouthparts were not dissected and examined in detail as I did not wish to damage the specimen. But they appear to be very similar to those of a Puerulus from the Marquesas represented in Fig. 6*a–e* except that the exopodite on maxilliped 2 is rather shorter, being about three-fourths of the merus. The mandibular palp is clearly seen without dissection.

Pereiopod I is appreciably shorter and somewhat more robust than the succeeding limb (Fig. 7*c*) ; the propodus is not quite three times as long as wide and the ratio of dactylus to propodus is 1 : 1·25 ; the merus is rather longer than carpus and propodus. Pereiopods II, III and IV are very similar in size and form, the propodus in each being almost exactly five times as long as wide ; the ratio of dactylus to propodus is 1 : 1·75–1·70 ; the merus equals propodus and carpus. The shrivelled remnant of the exopodite at the base of pereiopods I—IV is very small and is best seen when the limb (ischium to the tip) is detached, leaving the rudimentary exopodite exposed on the stump. Pereiopod V is the shortest and shows no trace of the exopodite ; the propodus is 5 times as long as wide.

Pleopod 1, that attached to the second abdominal somite, is represented in Fig. 3*e* ; most of the long setae on the exopodite and endopodite are omitted ; the *appendix interna* is long, and bears a subterminal plumose seta and a number of terminal coupling hooks (see enlarged view of apex).

Remarks. Unfortunately the post-larvae of the Palinuridae are seldom complete as to antennae, and this is especially true of those with long flagella. Several Puerulus stages, however, have been figured with the antennal flagellum tapering : e.g., that of *Panulirus argus* (Gurney, 1942, p. 234, fig. 93 ; Schmitt, 1935, p. 173, fig. 36 of the young crawfish), and I have examined the specimen figured by Gurney and find that the apex of the flagellum is as represented in Fig. 2*d* ; that of *P. regius* B. Capello (Schmitt, 1926, p. 43, fig. 67) ; of *P. japonicus* (Nakazawa, 1917, plate, figs. 3, 4, and 5 of the post-Peurulus). In these the antenna does not seem to exceed, if it attains, 1·5 times the body length.

Dr. Holthuis of the Leiden Museum kindly informed me by letter that a Puerulus with a long spatulate antennal flagellum had recently been described by Kubo in a paper written almost entirely in Japanese, but with a short summary in English (first paragraphs, p. 91—Kubo, 1950). As no copy of this paper was available in London, Dr. Holthuis sent me a photostat copy. (Later I received a reprint from the author—see p. 28.) Kubo attributes this Puerulus to *Panulirus "versicola"* (Latr.)—presumably a misprint for *versicolor*—and finishes his English abstract

as follows : " Some descriptions in regard to the puerulus of *P. versicola* have been given by Ortmann (1894) [error for 1891], Calman (1909), and de Man (1916). But no one has given description on the signal feature of the antennae."

Kubo's Puerulus is certainly very similar to that from Kenya ; his figures are small, and in the photostat copy some of the finer details are lost. The flagellum is just over twice the body length and ends in a spatulate expansion which is " stained with rather deep brown colour (in alcoholic specimens)," and I think his figure shows the brown band about one-third of the way along the flagellum. But I do not think that his Puerulus belongs to the same species as that from East Africa described above. As a rule his specimens have two pairs of spines, one in front of the other, at the anterior end of the lateral carinae and those behind the rostral horns are well formed. The general impression one gets from Kubo's figures is that the antennal and antennular peduncles are more robust than those of the Kenya specimen—more like those of specimens from the Marquesas described below (see p. 29 and Fig. 5*a*, *b*.). Nor do I think that Kubo is right in attributing all his post-larvae to *Panulirus versicolor* (Latr.) ; at any rate those figured do not agree with the specimens from Christmas Island which Dr. Calman (1909, p. 444) referred to that species (see p. 26).

I have found an earlier reference to a Puerulus with a spatulate apex to the antennal flagellum in a paper by W. von Bonde (1930, p. 25). In his specimen the antenna is also about twice the body length. The following extract may be quoted from von Bonde's paper : " NOTE.—Only one of my Puerulus specimens of *Panulirus* has the antennae intact. Each is developed at its distal extremity into a large flattened oar-like structure. Such an antenna has been figured by Richters (12) [error for (13)] in a large Phyllosoma (Ph. longicorne Guér., length 38 mm.)." Richters (1873, pl. xxxi, fig. 3) shows a last stage Phyllosoma with a long antenna, the clavate apex of which is rather wider than that represented in Fig. 2*b* and has no terminal spinose projection. The fragment represented in Fig. 2*b* was found in the jar along with a number of post-larvae and young from the Marquesas (see p. 29).

Thus several species of the genus *Panulirus* possess these spatulate antennae in the post-larval stage. Leach's type specimens of *Phyllosoma clavicorne* were collected in West African waters ; von Bonde's post-larvae, which he referred provisionally to *P. bürgeri* de Haan (= *homarus*), were from the East Coast of South Africa ; others are now known from Japan (Kubo, 1950), Kenya and the Marquesas. As von Bonde did not figure his specimens, I do not know from his description whether the antennules are like those of the Marquesas material (Fig. 5*b*), or more slender as in the Kenya specimen (Fig. 3*c*). But, as they are stated to have two pairs of branchial spines on the carapace they agree in this with the Marquesas Pueruli and it is probable that they are referable to *P. homarus* (L.). In the absence of post-Puerulus stages it is not possible to refer the Kenya specimen to the adult species, since it is not known whether abdominal grooves are present or absent. What can be said with certainty is that it belongs to a species with longer and more slender antennules than either *homarus* or *dasypus* (if the latter is regarded as a distinct species—see p. 35).

b. THE POST-LARVA OF *Panulirus versicolor* (LATR.)

(Fig. 4)

MATERIAL. Christmas Island, Indian Ocean. Dr. C. W. Andrews coll. partly on the reef and partly in crevices in the piles of the pier at Flying Fish Cove, reg. no. 1909.5.19.248–252. Five post-larvae.

(Also several later young crawfish stages, reg. no. 1909.5.19, 243–247).

DESCRIPTIVE NOTE. These specimens have been identified by Calman (1909, p. 444), and his determination is fairly certain since he had older stages, up to 74 mm. in length of body, collected at the same time and place. In none of his specimens is the antennal flagellum complete, but in one it exceeds 2·5 times the body length and yet shows no trace of expansion distally—thus it must be considerably longer than that of either the Kenya specimen described above, or of Kubo's post-larvae referred to "*P. versicola*" (Kubo, 1950, p. 94, fig. 3). De Man (1916, p. 61) says of his specimens "external antennae 3-times as long as the body"; this I at first regarded as a misprint for "2-times" (as Kubo may also have done), but Calman's material suggests that de Man's statement may be correct. If de Man's specimens were complete the apex of the flagellum was not spatulate or he would certainly have said so. I have since examined de Man's specimens in the Zoological Museum, Amsterdam. They certainly agree with our Christmas Island material but in none are the antennae now intact.

In all the post-larvae there are only three pairs of spinules on the carapace—one at the anterior end of the lateral carinae (not two, as in the majority of Kubo's specimens), one behind the orbits and one behind the supraorbital spines; in addition two pairs of incipient spinules are present on the cardiac region. They are thus similar to the specimen from Kenya except that the pair behind the rostral horns is distinct. The antennal peduncle is long and slender, rather like but not identical with that of the Kenya specimen (cf. Figs. 4*a*, *b* and 2*a*, 3*c*, *d*). The basal segment differs in that the portion containing the statocyst is shorter while the distal part is narrow and not expanded apically. A large round statolith is visible within the sac (as in all the post-larvae examined other than the one from Kenya, in which it may not have had time to form after a recent moult). Unfortunately, in all the specimens the antennal peduncle is partially collapsed on the inner surface, but it also is relatively long and slender. The pereiopods have also collapsed in most of the specimens, but in one they are normal and I and III are represented in Fig. 4*c*, at the same magnification as those of the other Pueruli. They are slightly longer than those of the Kenya specimen (Fig. 7*c*), or of the Marquesas material described below (Fig. 7*b*).

NOTE ON THE POST-PUERULUS AND LATER STAGES

As stated by Calman (1909, p. 444), the post-Pueruli are brown in colour, with a conspicuous W-shaped marking of white on the carapace and a transverse narrow white band on each abdominal somite, that on somite 1 on the anterior half, those on somites 2–6 parallel to the posterior margins. No abdominal grooves are present,

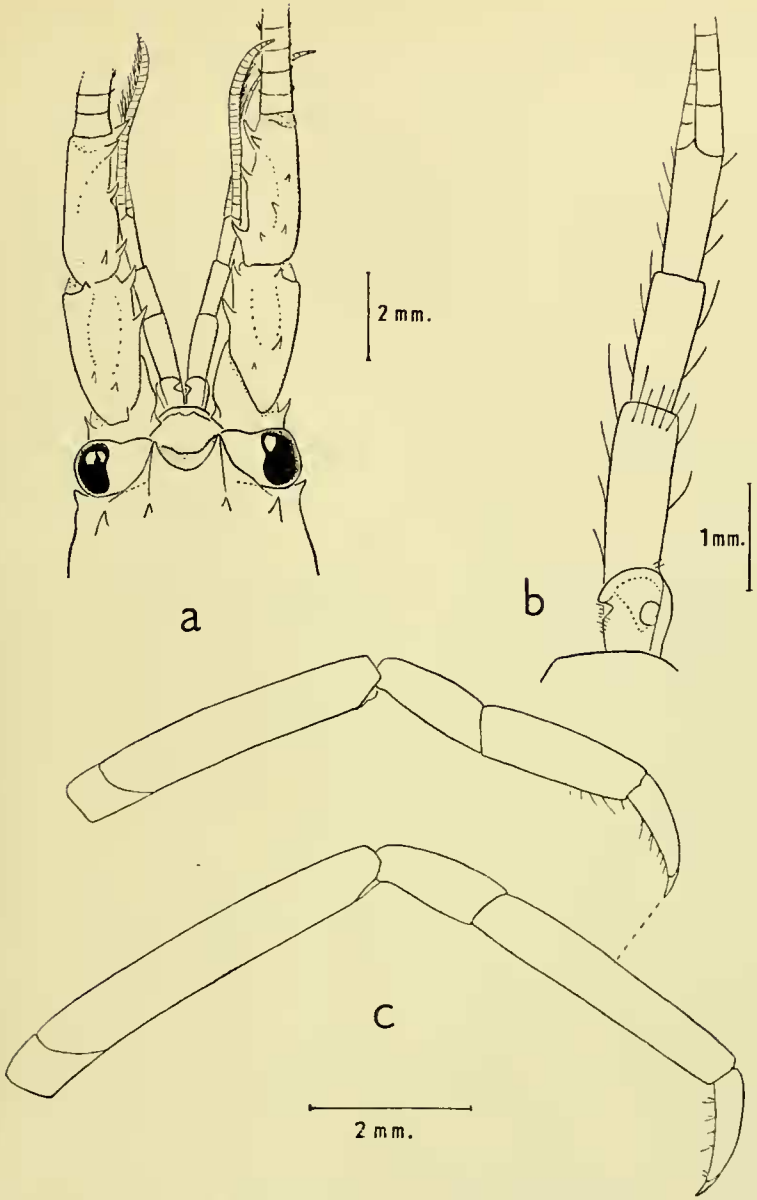

FIG. 4. Puerulus of *Panulirus versicolor* (Latr.) from Christmas Island. *a*. Anterior portion of carapace and antennal and antennular peduncles, in dorsal aspect. *b*. Antennular peduncle in dorsal aspect. *c*. Pereiopod I (upper) and pereiopod III.

as in the adult, but on each somite a number of transverse rows of minute pits, from each of which a short seta emerges, are present. A rather long forwardly directed seta arises from the base of several of the median spines on the carapace. After over 40 years in alcohol the colour pattern of these post-Pueruli is still clear.

In the two older stages from Christmas Island (*c.l.* 25 and 34 mm. respectively) the colour pattern is much nearer that of the adult ; the legs are striped, the dark purplish blotches on the carapace tend to obscure the short median bands of the W. The posterior whitish band across each abdominal somite is now flanked anteriorly and posteriorly by a purplish band. What is rather surprising, however, is the presence of a broad but very shallow transverse groove, with slight median interruption, on abdominal somite 2. The pits and setae are now confined to this area, the groove being filled with them while a few continue across the median break. On somite 3 there is a much wider median interruption, beset with sparse setae, between the two setose lateral grooves. On somite 4 there are just two short widely separated lateral patches of setae. Any setae on 5 and 6 are isolated and few in number. These broad shallow grooves on somites 2 and 3, or traces of them, are present in rather larger stages from other localities in the B.M. collection.

Remarks. As already mentioned on p. 25, I do not think that all Kubo's specimens belong to *P. versicolor* (Latr.). The antennal flagellum in the Puerulus of that species seems to be three times the body length and without a spatulate apex. Since I commenced this paper I have received a reprint from Dr. Kubo and I find that his fig. 4 o shows the W pattern rather faintly on the carapace of a young stage (this was not apparent in the photostat copy). I now think that part of Kubo's material only belongs to *P. versicolor*—namely the young with the characteristic pattern and perhaps the Pueruli which he lists with but *one* spine at the anterior end of each lateral carina (Kubo, 1950, p. 93, table 1). The other Pueruli which he figures, with two spines at anterior end of the lateral carina and the stouter antennal and antennular peduncles (Kubo, 1950, figs. 2 and 3) may belong to *P. homarus* (L.) like my specimens from the Marquesas. I do not know how many post-Puerulus and young stages Kubo had. But I assume that in his material no abdominal grooves were present, since that is the case in *P. versicolor*. In the post-Puerulus of *P. homarus* the abdominal grooves are present and show traces of the crenulation as well.

If Kubo's Puerulus with the spatulate antennae really has no abdominal grooves in the next stage, it might be referable to either *P. ornatus* (Fabr.) or *P. polyphagus* (Herbst). The adult of the latter species has a long multi-segmented flagellum on the exopodite of the second maxilliped as represented in Fig. 8*f*, and one would expect a well formed flagellum in the Puerulus also—as in that of *P. inflatus* (Bouvier) represented in Fig. 7*a*. Kubo's Fig. 4 k seems to have no flagellum, or a vestigial one as in fig. 6*d* perhaps. So that *P. polyphagus* would appear to be excluded. On the other hand, *P. ornatus* does not appear to have been recorded from Japanese waters, although it goes as far north as Formosa (Holthuis, 1946, p. 141.).

c. THE POST-LARVA OF *Panulirus homarus* (L.)

(Figs. 2*b–d* ; 5*a*, *b* ; 6 ; 7*b*)

MATERIAL. (*a*) Marquesas. " St. George " Expedition. W. 38.27.12.24. One Puerulus.

(*b*) Marquesas ; sand of beach, Hana Hevané. C. Crossland coll. 1925–26. Twenty four Pueruli, nine post-Pueruli and young crawfish stages up to 33 mm. in body length.

DESCRIPTIVE NOTES. The 25 Puerulus stages vary in body length from 22 to 24 mm. As each specimen has a narrow band of brown pigment some distance along the antennal flagellum, I thought at first that they must be identical with the specimen from Kenya described above. The antennal flagellum in some specimens shows a hint of expansion of the segments at the broken distal end (Fig. 2*c* and *c'*) and the flagellum in these is nearly twice the body length. My suspicion that the apex of the flagellum must be spatulate was confirmed in a rather unexpected way. Lying in the jar amongst detached limbs was the distal end of the antennal flagellum of the last stage Phyllosoma represented in Fig. 2*b*. The larval flagellum is unsegmented, but within this can be seen the fully formed flagellum of the Puerulus with the segmentation faintly visible through the chitin. It is obvious that the apex of this flagellum would be spatulate. Presumably this portion of the larval antenna broke off just before or during the critical moult from larva to post-larva. The apex of the larval antenna is very similar to that of the last stage *Phyllosoma clavicorne* Leach, the types of which are in the British Museum collection. The antennal flagellum of these Puerulus stages, therefore, seems to agree with that of the specimen from Kenya.

But on closer examination they were found to differ from the latter in a number of characters. The resemblances are many, chiefly in characters common to nearly all the *Panulirus* post-larvae that have been described such as the presence of the posterior pair of spines on the thoracic sternum. The chief differences are as follows : (i) In all specimens, even the smallest, four pairs of spinules are present on the carapace in addition to the spinose anterolateral angles, namely, a post-ocular pair, a postrostral pair, and two pairs one behind the other at the anterior ends of the lateral carinae. Two pairs of incipient spinules are present on the gastric region as in the Kenya specimen. (ii) The antennules are more robust ; the flagella have some 25 and 23 segments respectively ; the segments of the peduncle are in the ratio of 2 : 1 : 1, as seems usual at this stage, but each segment is broader relatively to its length (cf. Figs. 5*b* and 3*c*, *d*). The first segment is 2·5 times as long as wide, the portion containing the statocyst is nearly as long as the distal portion and a conspicuous statolith is always present. In the specimen from Kenya the basal segment is 4 times as long as wide and no statolith was visible. (iii) The antennal peduncle is shorter and more robust. (iv) The pereiopods also seem to be somewhat stouter, especially as regards the merus (cf. Fig. 7*b* and *c*). The mouthparts are represented in Fig. 6*a–e*.

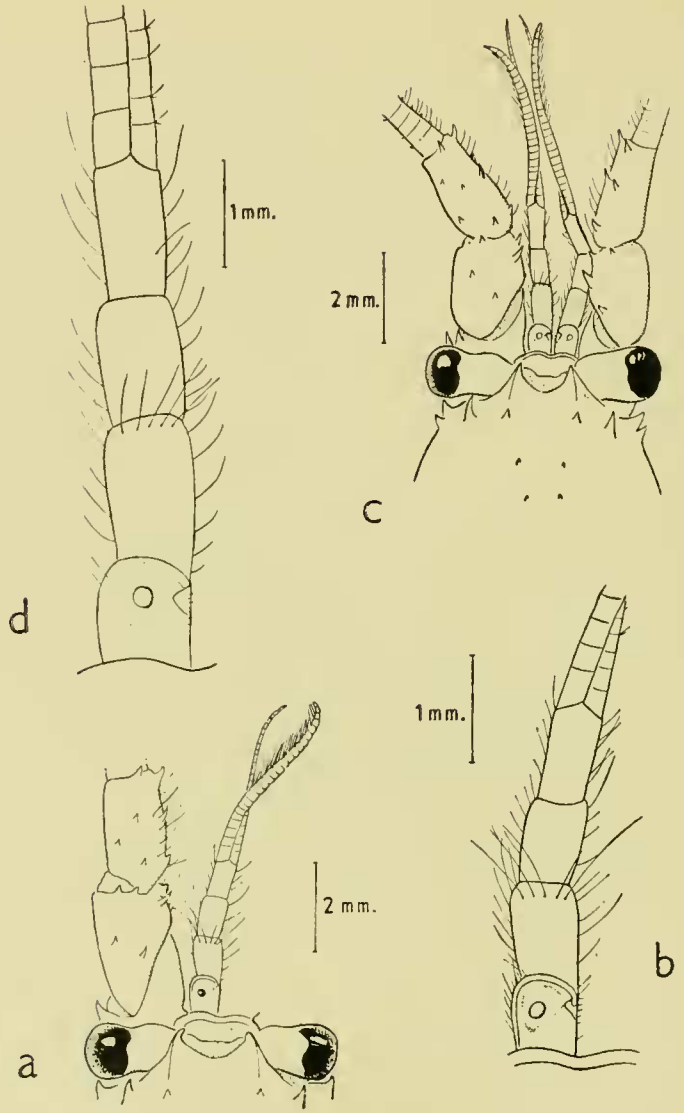

FIG. 5. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *a*. Anterior part of carapace with left antennal and antennular peduncles, in dorsal aspect. *b*. Antennal peduncle. Puerulus of *Panulirus inflatus* (Bouvier) from Coiba. *c*. Anterior part of carapace, antennal and antennular peduncles, in dorsal aspect. *d*. Antennal peduncle.

Remarks. Because several later stages are represented it seems possible to refer these young specimens to the adult species. These young crawfish possess an abdominal groove on each somite, and, moreover, crenulations are present in the older specimens in the lateral portions of each groove. The furrows are slightly interrupted in the centre on the second and subsequent somites. The largest young crawfish measures only 33 mm. from tip of supraorbital spine to tip of telson, but it has a tiny anterodorsal spine on the merus, near the distal articulation, of pereiopods II and III. The soft part of the telson is almost as wide as the hard basal portion ; pereiopod III is longer than pereiopod II by half the length of the dactylus ; the antennular peduncle is now very nearly equal to the antennal peduncle, and the basal segment of the former reaches almost to the distal end of the penultimate segment of the latter. Only one pair of slender spines are present on the antennular tergum at this stage. Many spines are present on the carapace. Holthuis (1946, pp. 110–112) lists the following species as widely distributed in the Indo-Pacific region : *Panulirus dasypus* (Latr.), *P. homarus* (L.), *P. japonicus* (von Siebold), *P. ornatus* (Fabr.), *P. penicillatus* (Oliv.), *P. polyphagus* (Herbst) and *P. versicolor* (Latr.). Of these the species without abdominal grooves or furrows may be excluded, leaving four—*dasypus*, *homarus*, *japonicus* and *penicillatus*. The post-larva of *P. japonicus* has been described by Nakazawa (1917, figs. 3, 4, and 5) ; he figures the antennae of the Puerulus as not exceeding 1·5 times the body length and tapering distally. According to Bouvier (1913, p. 87, key) there are no posterolateral spines on the thoracic sternum in "*Puerulus pellucidus*," which is referred to *P. japonicus*. In any case the antennule of the adult *japonicus* (de Haan, 1833–49, pl. 41/42) has an unusually long slender basal segment to the peduncle, equal in length to the sum of the three segments of the antennal peduncle, and one would expect the specimens from the Marquesas to belong to a species with a relatively short robust antennule. *P. penicillatus* can also be excluded because (i) the margins of the abdominal grooves are never crenulate, and (ii) there is in the adult a short but distinct exopodite on maxilliped 3 so that in the post-larva one would expect the exopodite to be larger than it is in these specimens. As the grooves on the abdominal somites are already distinctly crenulate laterally and slightly interrupted in the median line I have no hesitation in referring these young stages to either *P. homarus* or *P. dasypus*. Most authors are agreed that these two species are very closely related and, in the Appendix, I give reasons for believing that they belong to one rather variable species to which the older name *P. homarus* (L.) should be given.

A short description, without figures, of the Puerulus and post-Puerulus stages of *Panulirus dasypus* from the Red Sea was given by Bouvier (1913, p. 84 ; key to the known Pueruli of the Palinuridae, p. 87). These specimens were found " dans les crevasses du rivage, à Djiboutil " (Bouvier, 1913, p. 88, and 1914, p. 191). These young stages appear to be inhabitants of the littoral zone. The presence of crenulations and slight interruptions on the abdominal grooves at this stages does not necessarily mean that the grooves and sculpturing of the adults will remain of the B-form (or *dasypus* form)—see p. 38.

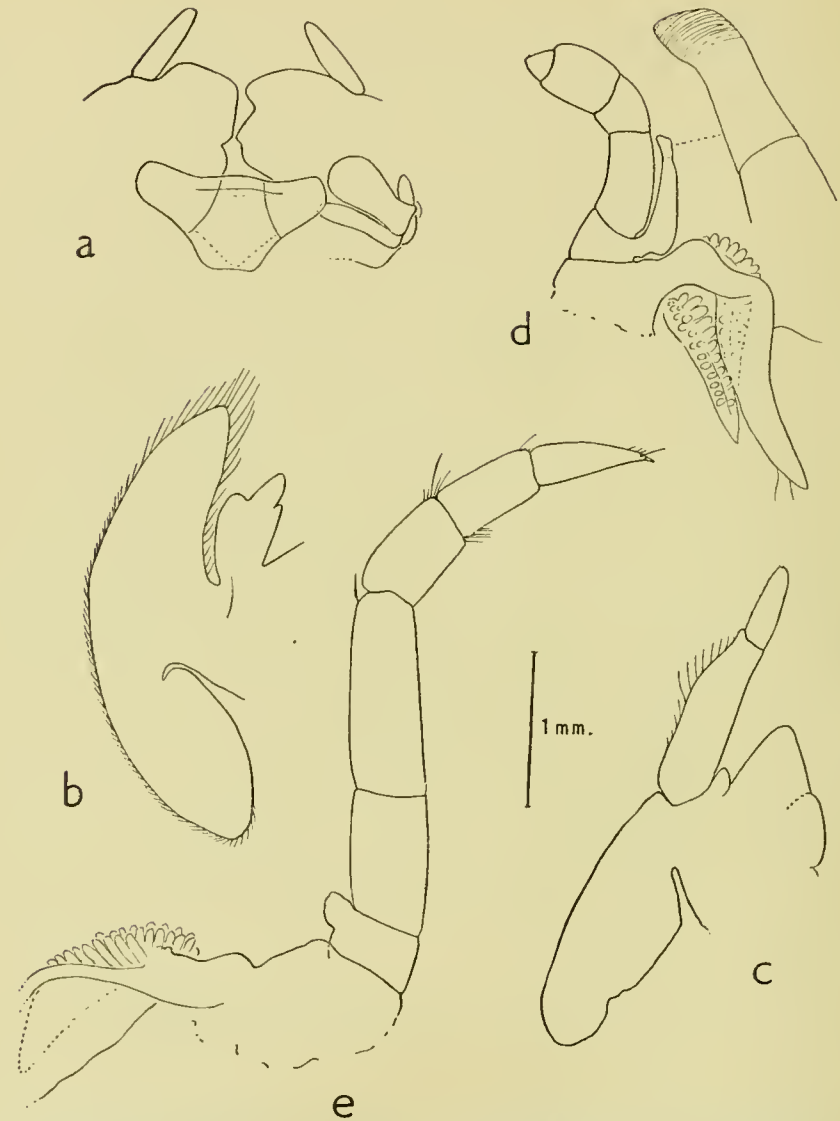

FIG. 6. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *a*. Mandibles, left maxillule and lower lip. *b*. Maxilla. *c*. First maxilliped. *d*. Second maxilliped. *e*. Third maxilliped (distal part of epipodite omitted).

d. THE POST-LARVA OF *Panulirus inflatus* (Bouvier)

(Figs. 5*c*, *d* ; 7*a*)

Material. Coiba Island. " St. George " Expedition 1924–25. One specimen measuring 22 mm. in length.

Description. This specimen has the carapace more swollen and distorted than usual. It agrees with most of the Pueruli that I have examined in having a pair of posterolateral spines on the thoracic sternum near the bases of pereiopods V. It differs from all the others in having *two* spines, one immediately behind the other, on each anterolateral angle of the carapace (Fig. 5*c*) and a backwardly directed spine at the posterior end of the median carina, i.e., on the posterior margin of the carapace. In addition to the spinules shown in Fig. 5*c*, namely, at the anterolateral angles, behind the orbits and supraorbital spines respectively, and two very minute pairs on the gastric region, there is only one at the anterior end of each lateral carina.

The antennae are unfortunately incomplete, so that the nature of the apex is unknown ; the longer exceeds 1·5 times the body length and shows no trace of any expansion—which does not necessarily mean that the apex is tapering. The details of the antennular and antennal peduncles are shown in Fig. 5*c* and *d* ; the former is more robust than that of the Puerulus from Kenya, or of the specimens referred to *P. versicolor* (Latr.). They recall those of the post-larvae from the Marquesas described above ; the region of the statocyst is rather opaque but the round statolith is visible. The mouthparts have not been examined in detail, but there is just a vestige of the exopodite on maxilliped 3 (as in Fig. 6*e*). The exopodite of maxilliped 2 has a long flagellum, and in this respect differs from that of the Marquesas material (cf. Fig. 7*a* and 6*d*).

Remarks. According to Holthuis (1946, pp. 110–111) there are but two species from the Pacific Coast of Central America, namely, *P. inflatus* (Bouvier) and *P. interruptus* (Randall). The latter species possesses in the adult the longest exopodite to maxilliped 3 of all *Panulirus* species and therefore its post-larva should have an even longer exopodite than that of, e.g., *P. argus* (Latr.) figured by Gurney (1942, p. 234, fig. 93E). Since the adult of *P. inflatus* lacks the exopodite on maxilliped 3 and has a large multi-articulate flagellum on the exopodite of maxilliped 2, I have no hesitation in referring this Puerulus to that species.

Amongst the registered post-larvae in the B.M. collection there is another specimen from Esmeraldas, Ecuador (reg. no. 1925.12.8.4), which also belongs to *P. inflatus*. The carapace is normal, and again there is a double spine at each anterolateral angle, but the posterior spine, that at the distal end of the median carina, is lacking. The antennal flagella are incomplete, and there is a rather broad band of brown pigment, a considerable distance from the peduncle, on the left side only. In both specimens there are two rows of 3–4 minute spinules on the proximal half of the soft part of the telson ; no spinules are present in the post-larva from Kenya (Fig. 2*a*) ; in the Pueruli of *P. homarus* there may be two pairs of minute spinules

in some of the specimens ; a few spinules are also present in some of the post-larvae of *P. versicolor*.

The holotype of " *Puerulus inermis* " Pocock, said to be the post-larva of *Panulirus guttatus* (Latr.) (Holthuis, 1946, p. 110), has the antennular peduncle of the shorter

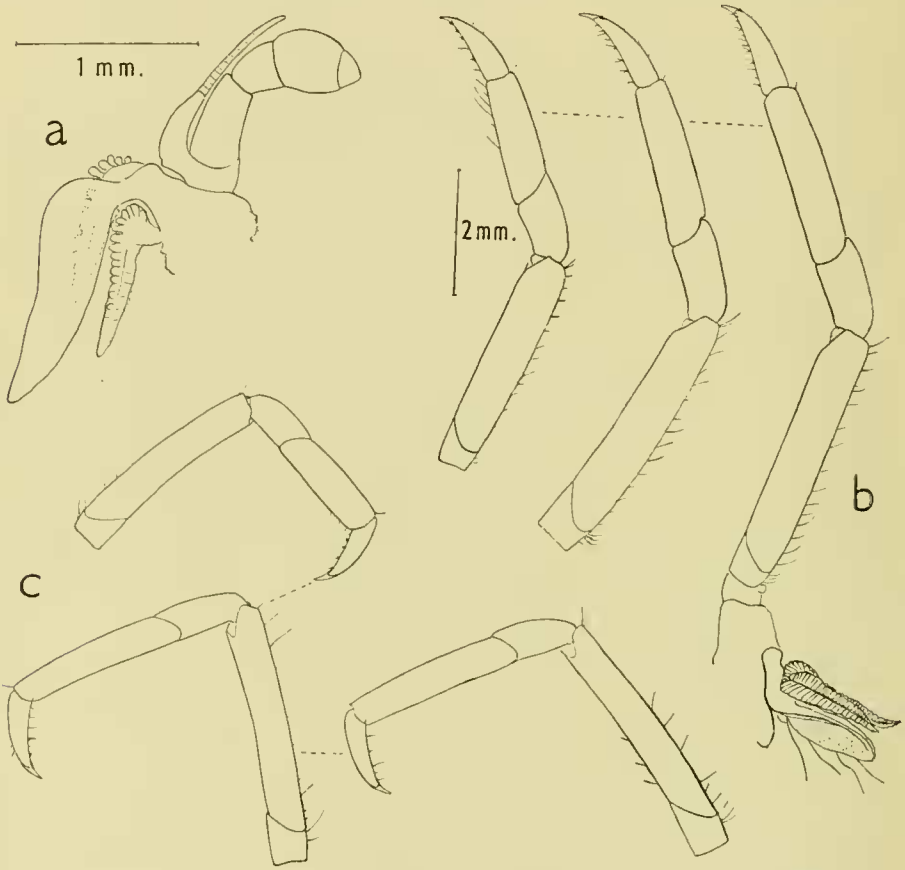

FIG. 7. Puerulus of *Panulirus inflatus* (Bouvier) from Coiba. *a*. Right maxilliped 2. Puerulus of *Panulirus homarus* (L.) from the Marquesas. *b*. Pereiopods I, II and III (from left to right). Puerulus of *Panulirus* sp. from Kenya. *c*. Pereiopods I (above), II and III.

broader form found in *P. homarus* and *P. inflatus* (Fig. 5*a–d*). The exopodite of maxilliped 2 has a shorter flagellum than that of the Puerulus of *P. inflatus* (Fig. 7*a*) and does not reach beyond the distal third of the carpus of the endopodite. The exopodite of maxilliped 3 is vestigial, as in Fig. 6*e*. The antennal flagellum is

incomplete. Pocock's specimen was dredged in about 10 fms. in Water Bay, Fernando Noronha (Pocock, 1890, p. 516).

APPENDIX

Note on Variation of the Adults of *Panulirus homarus* (L.)

(Figs. 8 ; 9)

Two Indo-Pacific species of *Panulirus*, namely *P. homarus* (L.)—better known as *P. bürgeri* (de Haan)—and *P. dasypus* (Latreille), are apparently very closely related. The differences between them are indicated in the following extract from Gruvel's key (1911, p. 50) :

> " Exopodite des deuxième maxillipèdes *avec fouet atrophié*. Sillons des tergites abdominaux toujours dentelés et nettement *ininterrompus*
> 4. *P. bürgeri*, de Haan.
> " Exopodite des deuxième maxillipèdes *sans fouet*. Sillons des tergites abdominaux dentelés et toujours au moins légèrement interrompus sur la ligne médiane
> 5. *P. dasypus*, Latreille."

Recently Holthuis (1946, pp. 128–136) has attempted to find clear-cut characters by which the two species may be separated ; he lists only some minor differences, and sums up by saying that more abundant material may perhaps show that the two are identical. In recent years I have had considerable correspondence with Dr. Leakey, of the Coryndon Museum, Nairobi, relating to the East African species, and from time to time he has sent me a few specimens for determination. Some of these seemed to agree with *P. homarus*, others with *P. dasypus* as far as the abdominal grooves were concerned, but, as Dr. Leakey pointed out, not always as regards the second maxilliped. For example, two specimens with the deep crenulation and uninterrupted furrows typical of *P. homarus* differed as to the exopodite of maxilliped 2 ; in one a small one-segmented flagellum was present as in Fig. 8*d*, whereas in the other the flagellum was absent as in Fig. 8*c*. The former therefore agreed with Gruvel's definition of *P. bürgeri* (avec fouet atrophié), while the latter agreed with that of *P. dasypus* (sans fouet). Two other specimens with the crenulation much less marked, especially mid dorsally, differed as follows : one was of a reddish colour, with uninterrupted grooves and no flagellum on the exopodite of maxilliped 2 (as in Fig. 8*c*) ; the other was bluish green, with a short but distinct median interruption of the groove on somites 2, 3 and 4 respectively, whereas the exopodite of maxilliped 2 has a large flagellum. (In 1948 I did not observe that the flagellum differed on right and left sides : that on the right is represented in Fig. 8*a* ; the flagellum can scarcely be described as " atrophié," being half the length of the basal segment of the exopodite and rather irregularly segmented ; that on the left is as represented in Fig. 8*d* and " atrophié.")

I have now re-examined the spirit specimens in the British Museum collection that have been referred to *P. bürgeri* (de Haan) and *P. dasypus* (Latreille) by Dr. Calman, who revised the material of *Panulirus* at one time (unpublished), and by

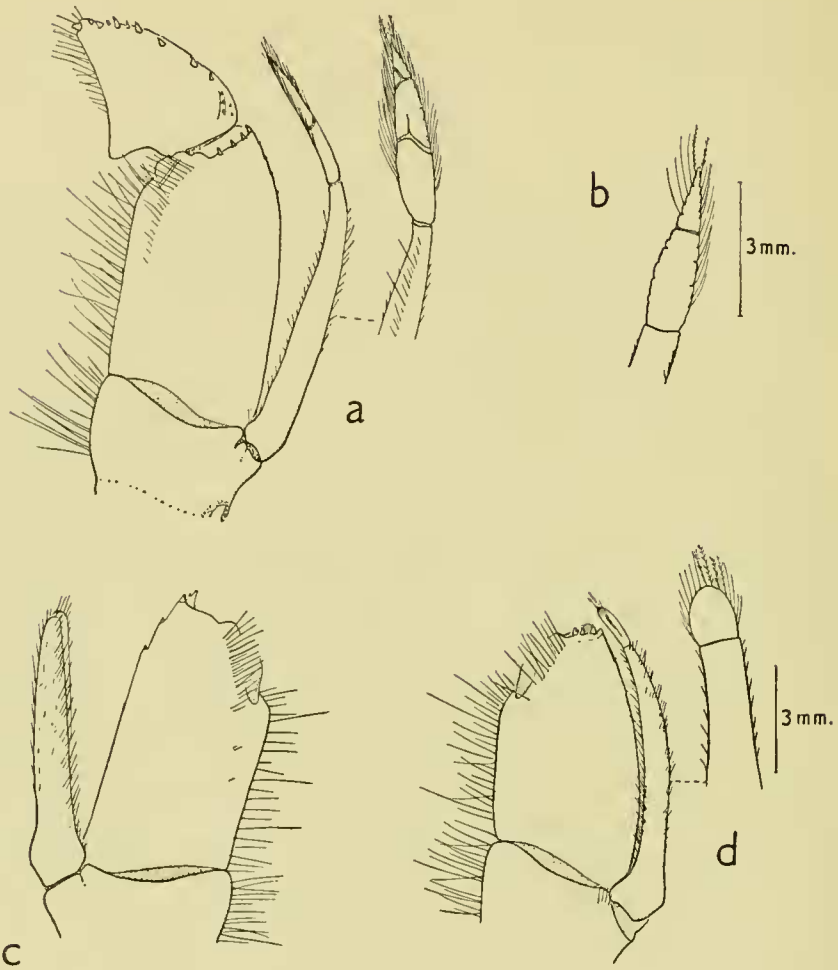

FIG. 8. Portions of the second maxilliped, in anterior aspect, to show the exopodite in various species of *Panulirus*. *a–f*. Adults, *g* and *h* very young specimens.

Panulirus homarus (L.). *a*. From specimen no. 3 in Table, with distal part of exopodite from the side normally facing the endopodite. *b*. Distal part of exopodite of right maxilliped of specimen no. 9. *c*. Left maxilliped of specimen no. 4. *d*. From specimen no. 6. *e*. From specimen no. 1. *g*. Right maxilliped of largest young stage from the Marquesas (*c.l.* = 13 mm.).

Panulirus polyphagus (Herbst). *f*. Left maxilliped of a ♀ (*c.l.* = 66 mm.) with the flagellum, in inner aspect, more enlarged.

Panulirus versicolor (Latr.). *h*. Right maxilliped of a young specimen (*c.l.* = 25 mm.) from Christmas Island.

myself. Unfortunately there are only fifteen specimens, three of which were referred by Dr. Calman to *dasypus* and eight to *bürgeri*, the remaining four being those already mentioned from East Africa. Table I shows briefly the variation in (*a*) the abdominal grooves and the sculpturing in their vicinity, and (*b*) the exopodite

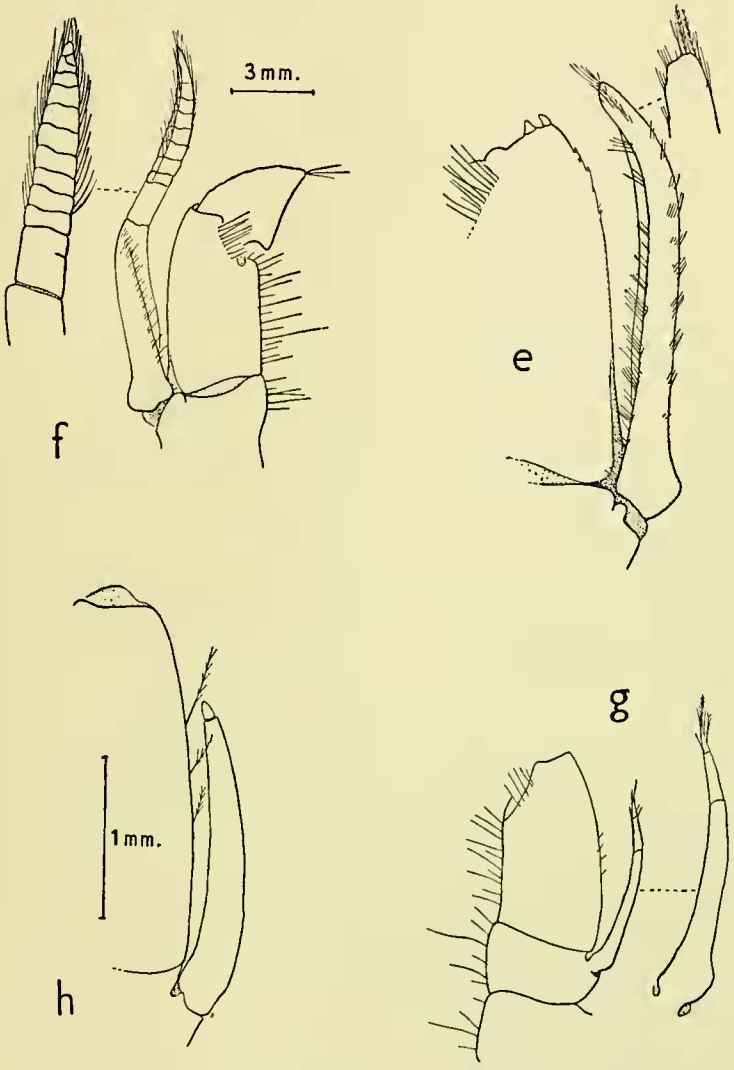

FIG. 8—*e-h*.

of the second maxilliped, exhibited by the twelve specimens which obviously belong to the *bürgeri-dasypus* complex. At first I thought that the six specimens with the

TABLE I

Panulirus homarus (= *bürgeri*)—specimens in B.M. Collection.[1]

No.	Sex	*c.l.* in mm.	Reg. no. Locality	Abdominal grooves and sculpturing	Exopodite of second maxilliped		
					Flagellum	Form of flagellum	
1	♂	105	1906.5.29.36 Socotra	A ++	Absent	R.	Fig. 8*e*.
						L.	As in Fig. 8*e*.
2	♂	*c.* 90	1948.3.12.1 E. Africa	B +	,,	R. L.	Alike—as in Fig. 8*c*.
3	♂	*c.* 88	1948.3.12.2 E. Africa	B + 2, 3, 4	Present (dissimilar)	R.	Fig. 8*a*.
						L.	As in Fig. 8*d*.
4	♂	88	Kenya, 1950	A +	Absent	R. L.	Alike—as in Fig. 8*c*.
5	♂	81	1925.8.18.87 Off Natal	A	,,	R. L.	Ditto.
6	♀	80	Kenya, 1950	A +	Present (similar)	R.	Fig. 8*d*.
						L.	As in Fig. 8*d*.
7	♀ ovig.	75	28/xi/08 No data	B + 2, 3	Present (dissimilar)	R.	Fig. 9*a*.
						L.	Fig. 9*a'*.
8	♀ juv.	61	1925.8.18.86 Off Natal	A +	Absent	R.	As in Fig. 8*e*.
						L.	Like R, but slightly shorter.
9	♀ juv.	60	1910.3.29.36 Goram Id.	B 2, 3	Present (similar)	R.	Fig. 8*b*.
						L.	As in Fig. 8*b*.
10	♀ juv.	57	1928.12.1.36 S. Africa	A	Absent	R. L.	Alike—as in Fig. 8*c*.
11	♂ juv.	50	80.6 Amboina	B	Present (similar)	R. L.	Alike—as in Fig. 8*d*.
12	♂ juv.	38	820*a* Ceylon	B — 3, 4	R. absent L. present	R.	As in Fig. 8*c*.
						L.	As in Fig. 8*d*.

A ++. Crenulation and sculpturing very pronounced, of the "*megasculpta*" form.

A +. Intermediate between A and A ++ ; some additional sculpturing and crenulation on certain somites.

A. Crenulation well marked along entire anterior margin of each uninterrupted groove.

B. Crenulation moderately developed, most marked laterally, on anterior margin of groove.

B +. As for B, but with traces of pitting on somites 2 and 3, or 2–4.

B —. Crenulation faintly indicated laterally, fading out medially. Some specimens of the B-form show a slight median interruption of the grooves on the somites indicated below B.

R and L = right and left second maxilliped respectively.

c. l. is measured from tip of supraorbital spine to posterior margin ; in specimens 2 and 3 the supraorbital spines are damaged.

[1] Recently, in the Zoological Museums of Leiden and Amsterdam, I have examined the material referred to *P. homarus* and *P. dasypus*, and find that it is just as variable as regards mouthparts and abdominal grooves as the B.M. material.

A-form of grooves and sculpturing belonged to *bürgeri*, the other six with grooves and sculpturing of the B-form to *dasypus*. In five of the former the flagellum of maxilliped 2 is absent, whereas in five of the latter it is present on both sides or (in one instance) on one side only. But the fact that in three out of the twelve specimens the exopodites are *dissimilar* on right and left maxillipeds (nos. 3, 7 and 12), and that the three forms of exopodite are thus combined (flagellum present and either long and 2- to 3-segmented, or short and 1-segmented, or absent), proves that this distinction is untenable. I am forced to conclude that these twelve specimens belong to a single variable species, *P. bürgeri* (de Haan), which according to Holthuis must now be called *P. homarus* (L.). In all probability many, if not all, of the references to *P. dasypus* in the literature refer to the less crenulate form of *P. homarus* (this difference does not depend on size as far as one can see). Specimen no. 1 in the Table, from Socotra, is that referred to as *P. dasypus* in Pocock, 1903, p. 214 ; the sculpturing on the abdomen is very pronounced and of the "*megasculpta*" form and I have no hesitation in referring it to *bürgeri*. The exopodite of maxilliped 2 is as long as the merus and yet there is no trace of a suture near the apex (Fig. 8*e*) ; Monod & Petit (1929, fig. 3E) figure the exopodite as only half the length of the merus in their *P. dasypus*, so that the range of variation here is considerable. As this is the largest specimen, the spines on the carapace are rather worn, but they are not as few in number as in Gruvel's specimen of *dasypus* (1911, pl. ii, fig. 5). The anterodorsal spine on the merus of pereiopods II and III, with one exception, have almost entirely vanished, so I do not think that the presence or absence of these spines is of specific importance.

Another difference listed by Holthuis (1946, p. 135), namely that pereiopods II and III are about equal in *homarus* whereas III is appreciably the longer in *dasypus*, is, I think, capable of another explanation. In small specimens of *P. homarus*, irrespective of sex, the pereiopods are relatively short. In the juvenile from Goram Island, for example, pereiopod I reaches the distal end of the second segment of the antennal peduncle, II is just a trifle longer and III a trifle longer still, reaching the distal end of the third segment of the peduncle ; IV reaches the middle of the propodus of I. By the time the carapace has increased to 88 mm. in length (no. 3 in Table) all the legs are a little longer relatively to the antennal peduncle, but the difference between II and III is not marked ; I exceeds the second segment of the peduncle by its dactylus, while III exceeds I by rather more than its dactylus (by 24 mm.) and IV is now a trifle longer than I. In the largest specimen (no. 1) pereiopods I and IV are subequal and reach the distal end of segment 3 of the peduncle much as before, but II exceeds I by the dactylus and one-fourth of the propodus (33 mm.), while III, now clearly the longest, exceeds II by its dactylus (30 mm.) and I by 63 mm. This specimen thus exhibits the commencement of a feature peculiar to senile males at least. The difference gets more pronounced with age, and this may well account for the long third pereiopod in Gruvel's specimen of *P. dasypus* (1911, pl. ii, fig. 5). Gruvel does not mention the sex of the specimen in the legend to the figure, which is one-fourth natural size, giving a *c.l.* of about 200 mm. Recently, when I had occasion to name some large dried specimens for the Zanzibar Museum, I was much impressed by an extraordinary case of allo-

metric growth of pereiopods II and III in senile males of *Panulirus ornatus* (Fabr.). Perhaps the females also exhibit the same phenomenon in old age, but the specimens at my disposal happened to be males. Two that are now in the B.M. collection show the commencement of the differential rate of growth of pereiopods II and III, and a much later stage, respectively. In the smaller the *c.l.* is 134 mm.

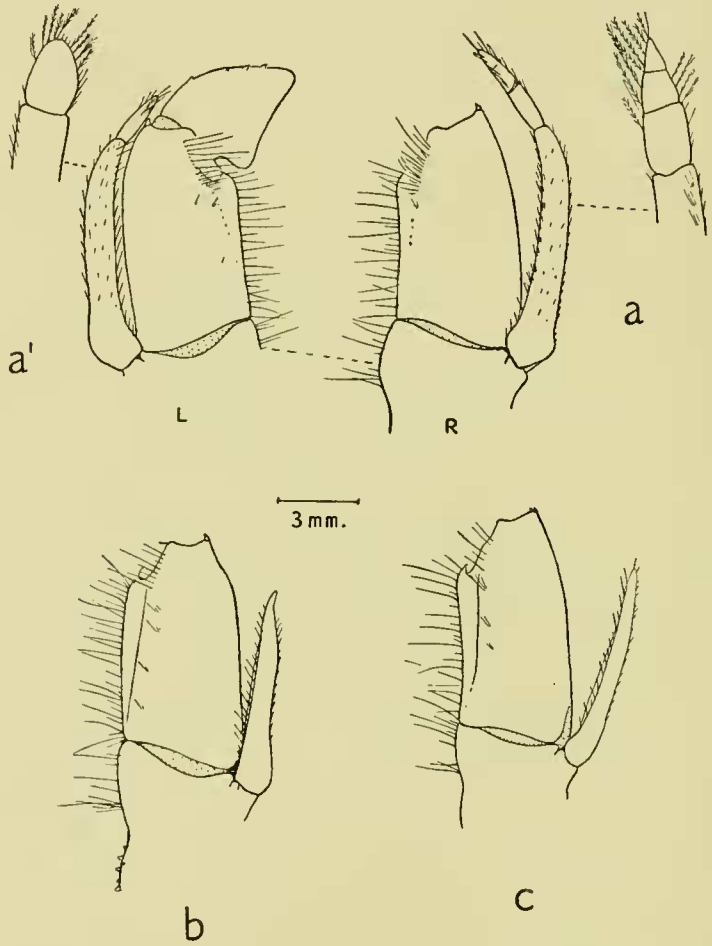

FIG. 9. *Panulirus homarus* (L.). *a* and *a'*. Right and left maxilliped 2 of specimen no. 7 in Table.

Panulirus ornatus ? (Fabr.). *b*. Right maxilliped of ♀ from Shanghai (*c.l.* = 76 mm., reg. no. 62.95). *c*. Same of ♀ from Swatow (*c.l.* = 72 mm., reg. no. 84.2).

and greatest *c.b.* is 85 mm. ; pereiopods I and IV are of equal length and probably scarcely reach beyond the distal end of the second segment of the antennal peduncle[1] ; pereiopod II exceeds I by rather more than the dactylus (32 mm.) ; pereiopod III exceeds I by the dactylus and some two-fifths of the propodus (55 mm.). The larger male with *c.l.* 170 mm. and greatest *c.b.* 130 mm. must have been about twice the live weight of the smaller one. Pereiopods I and IV are still equal and relatively short ; pereiopod II exceeds I by nearly all its propodus and the dactylus (about 115 mm.), while III exceeds I by some 186 mm.

Perhaps all species of the genus *Panulirus* will prove to undergo the same striking increase in length of some of the pereiopods in old age.

A well-developed exopodite, with long multiarticulate flagellum, on the second maxilliped is characteristic of some species, e.g., *Panulirus polyphagus* (Herbst)—unless, on re-examination of many specimens, the flagellum proves to be variable. This type of exopodite is presumably primitive, and there has been a tendency to reduction and loss of the flagellum within the genus. *P. homarus* would appear to be in process of losing the flagellum, which would explain the variation exhibited by the few specimens available. There are some dried specimens in the collection, but they are not suitable for a study of the mouthparts.

Finally, to return to the three specimens determined as *P. dasypus* by Dr. Calman, I am rather at a loss to know what to call them. They comprise two females from Shanghai and Swatow, China (*c.l.* 76 and 72 mm. respectively), and a young female from Palau Satang. In the juvenile the mouthparts are damaged ; the older specimens agree in having the exopodite of the second maxilliped shorter than the merus of the endopodite, and more slender than that of *P. homarus* (Fig. 9*b*, *c* ; c.f., Fig. 8*c*). The carapace is quite spiny and, in all three, abdominal grooves are present on somites 2 and 3, absent or evanescent on the posterior somites. There may be a median break or interruption, but the grooves are wider and shallower than in any of the *homarus* specimens examined, and filled with a fine short pubescence. When this is rubbed off one might overlook the grooves entirely and place the specimens in the subdivision without abdominal grooves. There is no trace of the crenulation which is always referred to in connection with *P. dasypus* and the antennular peduncle is relatively longer and more slender than in any of the specimens tabulated under *P. homarus*. These three specimens do not seem to agree with those referred to *dasypus* by Gruvel (1911, pl. ii, fig. 5), Monod & Petit (1929, p. 277, fig. 3 A–E) and others, and which appear to be the B-form of the variable *P. homarus* discussed above. Young specimens of *P. versicolor* have a broad shallow groove, filled with pubescence and with a median interruption, on somites 2 and 3, and just a trace of the setae on each side of somite 4 (see p. 28). These three specimens may belong to another species with abdominal grooves absent, as a rule, in adults—such as *P. ornatus* (Fabr.). Incidentally, there are records of *P. ornatus* from Swatow and Poeloe Satang, which is doubtless the same as Palau Satang—see Holthuis, 1946, p. 141. *P. ornatus* attains a very large size and might retain a juvenile character like these very shallow grooves for a considerable time.

[1] The pereiopods are all directed forwards and close together, while the antennae are bent back, as convenient for storing dried material, so that exact comparison is not possible.

These specimens are faded, but in the larger ones there are traces of the broad band of colour present on each abdominal somite of large specimens of *P. ornatus*.

REFERENCES

Bonde, W. von. 1932. Post-brephalus development of some South African Macrura. *Rep. Fish. Mar. Biol. Surv. S. Africa*, **8**, Special Rept. no. 1, 1930 [1932] : 1–42, 14 pls.

Bouvier, E. L. 1913. Le Stade " Natant " ou " Puerulus " des Palinuridés. *Trans. 2nd Intern. Congress Entomology, Oxford*, 1912 [1913], **2** : 78–89.

—— 1914. Recherches sur le développement post-embryonnaire de la Langouste commune (*Palinurus vulgaris*). *J. Mar. Biol. Ass. Plymouth*, n.s. **10** (2) : 179–193, 6 text-figs.

—— 1917. Crustacés décapodes (Macroures marcheurs) provenant des campagnes des yachts " Hirondelle " et " Princesse-Alice " (1885–1915). *Rés. camp. sci. Monaco, Paris*, **50** : 1–140, 11 plates.

—— 1925. Reports of the Results of Dredging . . . by the " Blake." XLVIII : Les Macroures Marcheurs. *Mem. Mus. Comp. Zool. Harvard*, **47** (5) : 401–472, 11 plates.

Calman, W. T. 1909. The genus *Puerulus* Ortmann, and the post-larval development of the Spiny Lobsters (Palinuridae). *Ann. Mag. Nat. Hist.* (8) **3** : 441–446.

Gilchrist, J. D. F. A post-puerulus stage of *Jasus lalandii* (Milne Edw.), Ortmann. *J. Linn. Soc. Lond. Zool.* **34** : 189–201, pls. 15 and 16, 13 text-figs.

Gruvel, A. 1911. Contribution à l'étude générale systématique et économique des Palinuridae. *Ann. Inst. océan. Monaco*, Paris, **3** (4) : 5–56, 6 pls.

Gurney, R. 1942. *Larvae of Decapod Crustacea.* Ray Society, vol. **129** (for the year 1941), pp. viii + 306, 122 text-figs. London.

Haan, W. de. 1833–50. Crustacea. [In P. F. de Siebold's *Fauna Japonica*] : 1–244, pls. 1–55 + A–Q.

Holthuis, L. B. 1946. The Decapoda Macrura of the " Snellius " Expedition : I. *Temminckia*, **7** : 1–178, pls. i–xi.

Kubo, I. 1950. On two forms of Puerulus found in Japanese waters, with special reference to that of *Panulirus versicola* (Latr.). *Bull. Japan Soc. sci. Fish.*, **16** (3) : 91–98, 4 text-figs., 2 tables.

Man, J. G. de. 1916. The Decapoda of the " Siboga " Expedition. Part III. Families Eryonidae, Palinuridae, Scyllaridae and Nephropsidae. *Siboga-Expeditie. Monographie*, **xxxix$_a^2$**, Leiden, 122 pp., 4 pls.

Monod, Th., & Petit, G. 1929. Contribution a l'étude de la Faune de Madagascar. Crustacea. II. Palinuridae. *Faune des Colonies Françaises*, **3** (4) : 269–291, 9 text-figs.

Nakazawa, K. 1917. On the metamorphosis of *Panulirus japonicus*. *Dobuts Z. Tokyo*, **29** : 259–267, 1 pl.

Ortmann, A. 1891. Die Decapoden-Krebse des Strassburger Museums . . . III. Die Abtheilungen der Reptantia Boas : Homaridea, Loricata und Thalassinidea. *Zool Jahrb., Jena, Abth. f. Syst.* **6** : 1–58, 1 pl.

Pocock, R. I. 1890. Crustacea. [In *Notes on the Zoology of Fernando Noronha*, by H. N. Ridley.] *J. Linn. Soc. Lond. Zool.*, **20** : pp. 506–526.

—— 1903. The Decapoda of Sokotra. [In *The Natural History of Sokotra and Abd-el-Kuri*, edited by Henry O. Forbes. *Special Bull. Liverpool Mus.* : 212–215, 1 text-fig.]

Richters, F. 1873. Die Phyllosomen. Ein Beitrag zur Entwicklingsgeschichte der Loricaten. *Zs. wiss. Zool. Leipzig*, **23** (4) : 623–646, pls. 31–34.

Schmitt, W. L. 1926. The Macruran, Anomuran, and Stomatopod Crustaceans collected by the American Museum Congo Expedition, 1909–1915. *Bull. Amer. Mus. Nat. Hist.*, **53** (1) : 1–67, 75 text-figs., 9 pls.

—— 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands. *Sci. Surv. P. Rico (New York Acad. Sci.)*, **15** (2) : 125–227, 80 text-figs.